

Table I. Weather data 1978–1980 mainly from Tromsø Meteorological Station. Averages are given for periods when snow cover was reduced to 0–4% on Tranøy.

	1978	1979	1980
Thaw on Tranøy ¹⁾	May 18	May 16	May 1
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Temperature (°C)			
May 7–15	1.8 (–5.7–10.6)	3.41 (–2.3–7.6)	3.21 (–1.3–7.5)
June 1–15	Myrberget, S., Olsvik, Ø. & Sæther, T. 1981: On a «crash» in a population of Willow Grouse <i>Lagopus lagopus</i> . <i>Fauna norv. Ser. C. Cinclus</i> 4, 64–68.		
June 16–30			15.707 5.2081
Precipitation (mm)			
June 1–15	From 1978–1980, Willow Grouse production on a small island in northern Norway was extremely bad in 1979. There were no noticeably high micro-rodent populations in the area during the period, but this grouse production «crash» could be predicted from rodent cycles in nearby areas. This «crash» could not have been caused by the influence of rodents on the spring food of the grouse.		
June 16–30			
For 1978 data by Tranøybun ²⁾			
For 1979 data by Tranøybun ²⁾			

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METHODS

INTRODUCTION

Most Norwegian Willow Grouse *Lagopus lagopus* autumn population levels show three to four year cyclic oscillations, which are largely in synchrony with variations in populations of small rodents such as voles and Lemmings *Lemmus lemmus* (Hagen 1952, Myrberget 1974). In some cycles, high grouse egg loss due to predation occurs in the rodent «crash» year following the rodent peak (e.g. Myrberget 1970, 1975a, 1980). Hagen (1952) suggested that in these springs there are fairly large numbers of grouse predators, produced during the rodent peak. After the rodent «crash», these predatory birds and mammals turn to alternative food such as grouse eggs and chicks.

Watson & Moss (1979) raised the question whether high predation in some years is due to changes in the predator situation or to changes in the grouse populations themselves. They noted that some studies of *Lagopus* spp. indicate that production losses are partly predetermined at egg-laying, due to variations in the quality of the hens' food in early spring. They further noted that in Scandinavia, both rodents and Willow Grouse eat heaths and scrubs, and they suggested that grazing by rodents may influence the food situation for grouse, and hence grouse numbers. If in this way the spring food of the grouse is particularly poor in rodent «crash» years, the hen's ability to withstand egg predators may be low, which may explain the high egg loss in these years.

¹⁾ It is difficult to test the validity of the latter

the springs 1978–1980. Voles were seldom caught by our dogs or seen during haymaking on the farm in any of the three years, and there were no breeding owls such as *Asio flammeus*.

Hypothesis by field experiments. This paper reports an experiment resulting from natural circumstances. In 1978 rodents were almost absent from our study area on Tranøy, but peaked in neighbouring localities. Thus any large rodent effect on plants on Tranøy in 1978 could be excluded. In 1978, three pairs in 1979 and in 1980. In 1978. Here follow some data on the Tranøy Willow Grouse population 1978–1980. Since Mårtensson & Höglund (1980) have shown that the synchrony between grouse and rodent cycles may be disturbed by weather particularly unfavourable to grouse, we also include certain meteorological data.

There was a noticeable increase in numbers of lepidopter larvae *Operophtera* sp. from 1978 to 1979. In 1980, the number of such larvae was so high that they destroyed most leaves of *Empetrum* sp. and *Vaccinium myrtillus* in the forest. Tranøy (69°09'N–17°25'E) is an island of 127 hectares in northern Norway (Troms county) located between the large island of Senja and the mainland (Myrberget 1975b). The study area also includes three small islets, total 10 hectares. Most of the Willow Grouse leave Tranøy in the beginning of September to winter on Senja (Myrberget 1978, 1975c, 1980). They return in March–April, while the production was poor in 1978. Hooded Crows *Corvus corone cornix* are the major egg predators, to a lesser extent Ravens *Corvus corax* and Magpies *Pica pica* (Myrberget lost at 1976). Stoats *Mustela erminea* take many grouse eggs in some years (Myrberget 1970).

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Table 1. Weather data 1978—1980 mainly from Tromsø Meteorological Station. Averages are given for periods. Extremes in brackets refer to minimum and maximum values actually recorded. Thaw refers to the date when snow cover was reduced to 3/4 of Tranøy.

	1978	1979	1980
Thaw on Tranøy ¹⁾	May 18	May 10	May 1
Snow depth (cm) May 15 ²⁾	81	13	0
Temperature $^{\circ}\text{C}$			
May 1—15	1.3(—5.7, 10.6)	3.4(—2.3, 7.6)	3.2(—1.5, 7.5)
June 1—15	7.9(2.0, 14.6)	7.8(3.0, 17.6)	8.1(0.6, 19.6)
June 16—30	14.1(1.5, 24.5)	10.8(5.4, 25.3)	15.7(7.5, 20.8)
Precipitation (mm)			
June 1—15	1.7(0, 16.5)	2.6(0, 8.6)	0.4(0, 14.5)
June 16—30	0.8(0, 10.2)	2.5(0, 8.0)	1.7(0, 16.9)

1) For 1978 data by Blom (pers.comm.). For 1979 and 1980 information from local inhabitants.

2) Tranøybotn II.

METHODS

The breeding population was censused in early June by the «pointing dog mapping method» (Myrberget 1976). When calculating egg-laying dates, we used an interval of one day between each egg laid and an incubation period of 21 days (Westerskov 1956). We distinguished between «normal» and «late» clutches. The latter category refers to nests where egg-laying started more than one week later than the annual mean.

Newly hatched chicks were claw-clipped at the nest using a code. Broods were located by a pointing dog, and the chicks were weighed.

Weather data were not systematically recorded on the island in the period. Standard meteorological observations from Tromsø (75 km NE) are used to describe the weather in the three years.

the springs 1978—1980. Voles were seldom caught by our dogs or seen during haymaking on the farm in any of the three years, and there were no breeding owls such as *Asio flammeus*.

On nearby Senja, however, the rodent populations reached a small peak in 1978, and there were high, peak populations in many other localities in Troms county (pers.obs. and H. Parker pers. comm.).

Two pairs of Hooded Crows nested in the area in 1978, three pairs in 1979 and in 1980. In 1978 flocks of 40 crows roosted on one of the islets. In May—June 1979 flocks of 50 crows and 12 Ravens visited the cultivated fields frequently to eat grain and peas. There were few flocking crows in 1980. In all three years 1—2 Magpies lived on the main island. Stoats were not observed during the study period.

There was a noticeable increase in numbers of lepidopter larvae *Operophtera* sp. from 1978 to 1979. In 1980, the number of such larvae was so high that they destroyed most leaves of *Empetrum* sp. and *Vaccinium myrtillus* in the forests.

RESULTS

The years — general characteristics

On Tranøy and on Senja (Tranøybotn) the thaw arrived much earlier in 1980 than in 1978 and 1979 (Tab. 1). In the standard period 1931—1960, temperatures in Tromsø averaged 3.0°C for 1—15 May, 7.5°C for 1—15 June and 10.1°C for 16—30 June. For the periods 1—15 May and 1—15 June the study years differ little from these averages. The latter half of June was much warmer than average in 1978 and 1980, and about average in 1979.

A few voles *Microtus agrestis* were observed in 1977, and a rodent peak was expected on Tranøy in 1978, four years after the previous peak in 1974. But there was no sign of vole grazing in

Grouse breeding data

The numbers of breeding grouse were: 18 hens and 17 cocks in 1978; 16 hens and 15 cocks in 1979; and 15 hens and 12 cocks in 1980. Tab. 2 shows that 1978 and 1980 were good breeding years in the area, while the production was poor in 1979.

In 1979, egg loss was very high, obviously largely due to predation by Hooded Crows. The loss was so high that we got few data for clutch size and egg-laying date. Only two of the 6 «nor-



Table 2. Breeding data (yearly averages) in 1978—1980. Number of examined clutches in brackets.

	1978	1979	1980
Date first egg laid	May 27 (7)	May 27 (3)	May 16 (10)
Clutch size «normal» period	11.9 (8)	9.6 (5)	12.2 (11)
Clutch size «late» period	7.5 (2)	6.0 (3)	10 (1)
Egg disappearance (%)	15 (10)	57 (9)	11 (12)
Chick mortality (%)	43 (10)	73 (7)	33 (10)

mal» nests found hatched. Three «late» nests were all successful. Two other pairs were found with broods. The 16 hens hatched 3 «normal» and 4 «late» clutches.

For 3 hens in 1979 there is no proof that eggs were ever produced, but we assume the hens had been robbed, either during egg-laying or early incubation, as they lived close to one crow nest. Also the observed grouse nest nearest to that crow pair was robbed. Another crow nest was predated in early June. Close to this pair there were two successful «late» grouse nests. We know that one of these hens had been robbed during egg-laying, and assume also the other. No grouse nested close to the third crow pair. Egg loss was also high on the islets, which are visited frequently by corvids.

Chick mortality was also high in 1979. Of 7 hatched broods we found only 3 with chicks older than one week. Net production was approximately 12 young, of which at least 9 came from «late» clutches.

The production of Willow Grouse was high in 1980, when 12 of the 15 hens had chicks, in one case from a «late» clutch. Another «late» clutch was deserted after we caught the hen. One nest was predated, and there are no breeding data for one hen. Average brood size at age 4 weeks was 7.7 (10 broods examined). Evidently no hen lost all her chicks. Net production was thus about 90 young.

Ten chicks from 5 broods of known age (6–20 days) were weighed in 1980. On average their weights corresponded with average weights given by Myrberget (1975d) for chicks 4 days older (extreme differences 2 to 6 days).

In 1980, when the thaw was early, egg-laying occurred much earlier than in 1978 and 1979 (Tabs. 1 and 2). There was no such clear relationship between time of thaw and clutch size and egg predation.

The survival of chicks was poorest in 1979 when the weather just after hatching was probably less favourable than in 1978 and 1980 (Tab. 3). No such relation is evident for the period just before hatching.

DISCUSSION

There was a slight decrease in the Tranøy breeding population from 1978 to 1980. In fact, the numbers breeding in 1980 were lower than ever recorded since the study started in 1960. Net production was poor in 1979 and the decline in 1980 thus expected. But since production was good in 1978, the decline in 1979 was unexpected in the light of earlier experience (Myrberget 1978). On Senja, however, the numbers of breeding Willow Grouse showed a marked increase from 1978 to 1979 (pers.obs.).

Compared to the average production rates for the area, 1960—1969 (Myrberget 1972), 1979

Table 3. Weather around time of hatching. Data for Tromsø. «Before» refers to averages for the 14 days just before mean hatching date. «After» is the mean hatching date and the following 9 days. Extremes in brackets. Rainfall on a «rainy» day is at least 0.5 mm.

	1978	1979	1980
Before hatching			
Temperature	12.7(1.5, 24.5)	10.4(5.4, 25.3)	7.3(0.6, 11.5)
Precipitation	0.80(, 10.2)	1.70(, 7.4)	0.30(, 1.6)
No. rainy days	2	6	4
After hatching			
Temperature	17.0(7.2, 25.5)	11.1(6.8, 19.1)	16.2(11.5, 20.8)
Precipitation	0.0(0, 0.4)	2.0(0, 8.0)	2.5(0, 16.9)
No. rainy days)	4	3

must be defined as an unusually bad production year, and 1978 and 1980 as very good years; 1980 in fact the best in the whole study period.

Egg predation in the area was higher in 1979 than in any other year, and variations in egg loss rate in 1978–1980 were as predicted, assuming a rodent peak in 1978. In 1979 predation of grouse eggs was extremely high near two Hooded Crow nests. This, along with evidence from other years (Myrberget et al. 1976, Erikstad et al. in press) suggests that on the main island it is predominantly territorial crows that take grouse eggs. Territorial crows numbered the same in 1979 and 1980, and it is unlikely that the great difference in egg loss can be explained by the relative localizations of crow and grouse nests in the two years.

Thus there was no clear relation between number of egg predators and egg loss, as suggested by Hagen (1952). We have no data on variations in available food for Hooded Crows, nor on the ability of grouse hens to withstand egg predation by crows in the different years. The cause of the varying egg predation is therefore not understood.

Chick mortality was also high in 1979. Annual variations in weather during the chicks' first days seem insufficient to explain the variations in chick mortality (cf. Marcström & Höglund 1980). Causes of chick mortality are unknown. Some chicks may be killed by birds like Ravens (Erikstad 1979). Data from previous years indicate, however, that much of the annual variation in chick mortality in the area is due to the same factors as govern chick body growth (Myrberget et al. 1977). One proposed explanation is that phenological development before hatching results in different food possibilities for the newly hatched chicks (Slagsvold 1975). The given meteorological data do not, however, support this hypothesis.

The only data on the chicks' food situation in the different years concern varying numbers of *Operophtera* larvae, a preferred and nutritious chick food in the area (Spidsø 1980). As the numbers of these caterpillars were higher in 1979 than in 1978, it is unlikely that lack of suitable food caused the high chick mortality in 1979. The exceptionally high number of these larvae in 1980, however, may be the main reason for the high rate of body growth of the chicks that year.

The causes of the varying yearly production rates are thus not understood. Since our data refer to one grouse cycle only, we can hardly expect to throw much light on the causes of cyclic

population levels in Norwegian Willow Grouse. The most important finding is that we could predict annual variations in production outputs of Willow Grouse from the knowledge of the pattern of cyclic variations in micro-rodent populations in nearby areas, even if voles were almost absent in the study area itself during the period. Thus the poor grouse production in 1979 could not have been caused by rodents influencing the grouse spring food.

The link between rodent and grouse cycles is still obscure. A complicating fact is that despite studies by numerous scientists, the causes of cyclic variations in rodent populations are still poorly understood (e.g. Stenseth 1978).

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SAMMENDRAG

Et «krakk-år» hos lirype på Tranøy i Troms

I 1978–1980 var reproduksjonen av lirype *Lagopus lagopus* på Tranøyå særlig dårlig i 1979. Det er tidligere kjent at slike «krakk-år» ofte kommer året etter at smågnagerne har hatt bestandstopp. Selv om det i perioden ikke var noen bestandstopp av smågnagere innen området, kunne dette «krakket» bli forutsagt ut fra kjennskap til svingninger i gnager-bestandene i andre områder i Troms. Smågnagerne kunne ikke ved sin beiting ha påvirket rypenes vårføde på Tranøy i forsøksperioden, og dermed slik ha forårsaket den dårlige rypeproduksjon i 1979.

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